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Original Article

Fecundity of giant freshwater prawn (*Macrobrachium rosenbergii*) varies with the trophic status and size of the inhabitant perennial reservoirs in Sri Lanka

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Abstract

Giant freshwater prawn (GFP, Macrobrachium rosenbergii) is an important commodity in the inland fisheries of Sri Lanka, where fecundity plays a crucial role in estimating the reproductive potential of the species. The fecundity of ovigerous GFP in relation to the trophic status and area of the reservoirs was empirically determined from the GFP collected from twenty-five dry-zone perennial reservoirs across Sri Lanka. Morphometric parameters, total and relative fecundity, and egg characteristics of ovigerous females were calculated. The total fecundity of GFP, which ranged between 5277±2069 - 29366±2371, differed significantly (p<0.05) with the trophic status and size of the reservoirs. The highest total fecundity was observed in the 24-25 cm and 185-210 g length and weight classes of GFP. The GFP inhabiting eutrophic medium perennial reservoirs exhibited the highest fecundity. Fecundity correlates with total length (r=0.75) and weight (r=0.71) of GFP. The total length of GFP was significantly associated with egg mass weight (r=0.74) in mesotrophic reservoirs compared to eutrophic reservoirs. Correlations between fecundity and body weight (r=0.70), fecundity and egg mass weight (r=0.76), egg mass weight and total length (r=0.69), and weight (r=0.72) were stronger in minor perennial reservoirs than in major and medium reservoirs. The present findings confirm that fecundity depends on the length, weight, and egg mass weight of ovigerous GFP, but not on the egg volume. The results align with the postulated hypothesis that the fecundity of ovigerous GFP varies with the trophic status and size of the reservoir.

Keywords: culture-based fisheries; eutrophic; length and weight; mesotrophic; relative fecundity

1 | INTRODUCTION

From the earliest recorded history, inland fisheries have played a significant role in the subsistence and self-supporting economy of Sri Lanka (Jones *et al.* 2021). Large-scale development of inland fisheries began only in

the early 1950s with the introduction of tilapia and carp species to the dry zone reservoirs of Sri Lanka. Developing culture-based fisheries (CBF) in village reservoirs is the most important inland fisheries enhancement strategy currently being implemented (Wijenayake *et al.* 2005).

Exotic tilapia, Chinese and Indian major carp, and the indigenous giant freshwater prawn (GFP) are the major commodities used for CBF in Sri Lanka's reservoirs (Deepananda et al. 2014). Consequently, culture-based capture fishery production has contributed over 50% (59838 Mt) of the total inland aquaculture production (90340 Mt) of the country by 2019 (Fisheries Statistics 2020). The GFP is a globally significant species, contributing up to 9% of total aquaculture production in 2016 (FAO 2018). In Sri Lanka, the production of GFP mainly occurs through CBF in the country's dry zone reservoirs. Since 2008, the National Aquaculture Development Authority of Sri Lanka (NAQDA) has been stocking post-larvae and fishers recapturing marketable-sized GFP as by-catch in reservoirs. An increase in production is crucial due to the high export potential and market price of GFP. The importance of GFP for commercial fisheries and aquaculture compels authorities and scientists to understand their ecology, biology, physiology, and behaviour (Rao 1991; Cavalli et al. 2001; Sithee et al. 2006).

Reproductive aspects are important in assessing the stock size of the GFP in Sri Lanka's reservoirs; however, such studies are scarce. The fecundity, governed by both intrinsic biological traits and extrinsic ecological factors, can be expressed as the total number of eggs a female produces during her average lifespan. It can also be presented as the number of ripening eggs in a female's ovaries before spawning (Shrivastava 1999). Biological factors influencing fecundity include body size, age, reproductive strategies, and morphological characteristics such as abdominal volume and pleopod length (Nazari et al. 2003; Arshad et al. 2006; Kawan et al. 2019). Environmental variables such as food availability, temperature, salinity, turbidity, dissolved oxygen (DO) levels, and seasonal shifts also play significant roles. Thus, individuals of the same species produce a varying number of eggs, depending on their age, length, weight, and environmental conditions (De 1980; Bal and Rao 1990). Notably, fecundity in aquatic species is often shaped by reservoir productivity, which is in turn influenced by the reservoir's trophic status and the concentration of nutrients that support primary production (Winemiller and Rose 1992). In Sri Lankan perennial reservoirs, variations in trophic status are primarily determined by phytoplankton biomass, which reflects the nutrient levels present in the water (Deepananda and Macusi 2012). Nutrient-rich environments enhance the availability of food at lower trophic levels (Warry et al. 2016) and improve growth and reproduction in higher organisms, such as GFP, which may potentially affect fecundity.

In Sri Lanka, GFP hatchery production is constrained by poor broodstock quality and low capacity, while wild populations are declining due to habitat degradation, pollution, and illegal fishing. Higher fecundity in GFP helps sustain post-larvae production and consequently increases population density after stocking. This is useful for estimating the number of spawners needed to produce a desired quantity of seeds for farming (Rashid et al. 2013). Understanding the fecundity of GFP in reservoirs is crucial for estimating the reproductive potential of brooders, which can significantly aid in implementing effective management strategies for prawn hatcheries. GFP in culture-based situations is expected to be confined to reservoirs with little or no access for spawning migration toward the ocean. However, observed aggregations near spillways, reported by local fishers, may suggest behaviour influenced by environmental gradients or structural features, which could align with habitat selection or spawning site preference known in other crustaceans. While fecundity has been widely studied in hatchery systems, little is known about the fecundity of wild or semiwild GFP in reservoir ecosystems, particularly in the context of reservoir trophic conditions. Hence, there is a clear gap in understanding the ecological determinants of reproductive success in culture-based GFP populations. Thus, the study aims to investigate the fecundity and relative fecundity of ovigerous GFP in perennial dry zone reservoirs of Sri Lanka, to elucidate the relationship with trophic status and reservoir size. Based on these observations, we hypothesize that the fecundity of GFP is positively influenced by both the trophic status and the size of the reservoir.

2 | METHODOLOGY

The study was conducted from 2021 to 2022 in twentyfive perennial dry-zone reservoirs in Anuradhapura, Puttalam, Hambantota, and Monaragala districts, which collectively accounted for 42.8% of Sri Lanka's total inland aquaculture fish production in 2020 (Fisheries Statistics 2021), highlighting their significance in GFP culture-based fisheries. The surface area (ha) of each reservoir was obtained from the National Aquaculture Development Authority of Sri Lanka (NAQDA), and the reservoirs were classified as major (>800 ha), medium (200 - 800 ha), and minor (<200 ha) perennial reservoirs (Wijenayake et al. 2021) (Table 1). For chlorophyll-a analysis, 150 mL of water was filtered through GF/C filters (1.2 µm, 47 mm diameter), and the filters were stored in acid-free, lightproof vials on ice before being taken to the laboratory. In the laboratory, filter papers were macerated in 90% acetone. Using a spectrophotometer, the absorption values of the acetone extraction were measured at 750 nm and 664 nm before acidification, and at 750 nm and 665 nm after acidification (Carlson and Simpson 1996). Carlson's trophic state index (TSI), based on chlorophyll-a content in the water, was used to estimate the trophic status of the reservoirs. Based on Sanuja et al. (2024), the study reservoirs were categorized into different trophic statuses (Table 1). TSI was calculated based on chlorophyll-a content using the following equations.

TSI (Chl-a) = 9.81 In Chlorophyll a (mg/m³) + 30.6 (Carlson and Simpson 1996)

Ten ovigerous GFP samples, collected from fishermen at each reservoir, were bought and transported to the laboratory within one day, stored in flake-ice-filled Styrofoam boxes. Upon arrival, a detailed analysis was immediately conducted. The total length (from the tip of the rostrum to the tip of the telson) and weight of each

specimen were recorded. Fecundity in the present study refers to the number of eggs found in the brood pouch during a single spawning. For brood fecundity analysis, eggs were gently separated from the second egg-bearing pleopod seta (Kumar *et al.* 2019), and the total egg mass from the abdomen was removed smoothly and carefully. The total egg mass was weighed using an analytical balance (SA220.R2, S/N-587289, RADWAG Wagi Elektroniczne).

TABLE 1 Detailed description of the study dry-zone reservoirs in Sri Lanka.

District	Reservoir	Surface area	Cina catagogy	GPS coordina	GPS coordinates			
DISTRICT	Reservoir	(ha)	Size category	North	East	Trophic status		
Anuradhapura	Nachchaduwa	1781	Major	8°14'57.61"	80°28'55.37"	Mesotrophy		
	Mahakanadarawa	1457	Major	8°23'42.65"	80°33'07.84"	Mesotrophy		
	Mahawilachchiya	971	Major	8°28'05.04"	80°11'46.78"	Mesotrophy		
	Angamuwa	445	Medium	8°10'27.49"	80°13'17.35"	Mesotrophy		
Puttalam	Thabbowa	607	Medium	8°04'00.34"	79°57'23.48"	Mesotrophy		
	Mahauswewa	212	Medium	7°55'37.36"	80°05'47.61"	Eutrophy		
	Saliyawewa	85	Minor	8°10'06.55"	80°05'38.89"	Mesotrophy		
	Pahariya	72	Minor	8°07'31.67"	79°59'46.04"	Mesotrophy		
	Kottukachchiya	70	Minor	7°55'39.29"	79°56'40.39"	Mesotrophy		
Hambantota	Ridiyagama	871	Major	6°12'15.17"	80°59'03.64"	Eutrophy		
	Weerawila	567	Medium	6°17'13.30"	81°13'57.39"	Eutrophy		
	Muruthawela	516	Medium	6°12'54.85"	80°43'27.13"	Eutrophy		
	Yodhawewa	486	Medium	6°16'14.46"	81°18'51.85"	Eutrophy		
	Bandagiriya	381	Medium	6°15'19.40"	81°08'20.14"	Eutrophy		
	Udukiriwala	263	Medium	6°09'20.52"	80°45'28.05"	Eutrophy		
	Pahala Andara	80	Minor	6°19'07.43"	81°06'46.82"	Eutrophy		
Monaragala	Muthukandiya	560	Medium	6°58'46.58"	81°30'07.66"	Eutrophy		
	Kiriibbanwewa	375	Medium	6°22'33.46"	80°58'13.66"	Mesotrophy		
	Urusita	262	Medium	6°19'55.17"	80°55'59.56"	Mesotrophy		
	Handapanagala	226	Medium	6°39'56.88"	81°09'07.00"	Mesotrophy		
	Hambegamuwa	210	Medium	6°32'33.69"	80°57'19.19"	Mesotrophy		
	Buduruwagala	145	Minor	6°41'15.59"	81°05'06.03"	Eutrophy		
	Habaralu	80	Minor	6°24'10.23"	80°55'09.67"	Mesotrophy		
	Mahawewa	80	Minor	6°27'29.93"	81°00'40.03"	Eutrophy		
	Sugaladevi	50	Minor	7°01'15.77"	81°35'28.14"	Mesotrophy		

Egg samples were dipped in 50 mL of Gilson's fluid and kept in the dark for at least two nights, as darkness is crucial for preserving Gilson's fluid, primarily to prevent the breakdown or alteration of the specimens being preserved (Davenport 1960). Bottles were vigorously shaken to disintegrate ovarian tissue and release individual eggs. Sample bottles were kept in the dark until further analysis. Individual fecundity was determined by counting the total eggs volumetrically using a 250 mL Stemple pipette. Since the number of eggs was high, the sub-sample method was used to estimate fecundity. A dissecting microscope (LEICA M26) was used to facilitate visualizing and counting eggs. Egg counting was performed in triplicate under constant volume (2.5 mL). Relative fecundity (per gram) was measured using the number of eggs per unit body weight, and the total (absolute) fecundity was the total number of eggs that were likely to be spawned in one spawning season. The relative fecundity was calculated using the following formula:

Relative fecundity = Total number of eggs in the brood pouch / Total wet weight of prawn (g)

Egg diameter (mm) was calculated using a calibrated ocular micrometre mounted on a compound microscope (Kyowa BIOLUX -12). Egg volume was measured using the equation following Nazari *et al.* (2003).

Egg volume (mm³) = $(\pi r^2 h) / 6$.

Where, r = length of short axis (mm), h = length of long axis (mm), $\pi = 3.14$

GFP with eggs was classified into length (1 cm) and weight (25 g) categories to get a distinguishable relation-

ship, and the total fecundity and relative fecundity for those size classes were calculated. Total fecundity and relative fecundity were evaluated for two different trophic statuses (mesotrophic and eutrophic) and three size categories (major, medium, and minor) of reservoirs. The reservoirs were further divided into size classes (200 ha) based on their surface area at full supply level to assess the changes in fecundity in relation to the reservoir size. The IBM SPSS Statistical Software package (version 25.0) was used to calculate all the descriptive statistics. After testing for data normality using the Shapiro-Wilk test, the non-parametric Mann-Whitney U test and Kruskal-Wallis test were employed to compare the mean fecundity values among the trophic status and size categories of the reservoirs, respectively. Additionally, correlations between variables were computed. The analysed data, presented as means \pm SD, were conveyed.

3 | RESULTS

Trophic statuses categorized the study reservoirs into either mesotrophy (n = 14) or eutrophy (n = 11), with no oligotrophic reservoirs identified. Total fecundity, relative fecundity, and volume of an egg of the GFP inhabiting in reservoirs of four districts (Anuradhapura, Puttalam,

Hambantota, and Monaragala) were significantly different (p < 0.05), albeit total length, body weight, and egg weight of the GFP (n = 250) were statistically indistinguishable (p > 0.05). The mean total weight and length of berried GFP ranged from 74.20 ± 3.48 g to 240.37 ± 44.69 g, and 20.30 ± 0.66 cm to 29.8 ± 1.6 cm, respectively. GFP from Mahakanadarawa and Badagiriya reservoirs showed the greatest weight and length, respectively, while the GFP from Mahawilachchiya exhibited the lowest weight and length. The egg mass weight of GFP ranged from 7.17 \pm 2.70 g (Mahawewa) to 20.61 \pm 7.08 g (Kottukachchiya), while the volume of an egg ranged from 0.04 ± 0.01 cm³ (Muthukandiya and Buduruwagala) to 0.19 ± 0.13 cm³ (Angamuwa). The highest total fecundity (29366.67 ± 2371.36) and relative fecundity of the berried GFP (232.24 ± 22.43) were recorded from Yodhawewa, while the lowest total fecundity and relative fecundity were reported from Saliyawewa (5277.78 ± 2069.44) and Angamuwa (45.00 ± 10.44), respectively. The mean body weight, total length, egg mass weight, volume of an egg, total fecundity, and relative fecundity of berried GFP collected from 25 reservoirs in four study districts of Sri Lanka are summarized in Table 2.

TABLE 2 Body weight, total length, egg mass weight, the volume of an egg, total fecundity, and relative fecundity of giant freshwater prawn collected from perennial reservoirs of Sri Lanka (M, mesotrophic; E, eutrophic; MAP, major perennial; MEP, medium perennial; MIP, minor perennial; values are presented as mean ± SD).

Location and res-	Trophic	Reservoir	Body weight	Total length	Egg mass	Volume of	Total fe-	Relative fe-
ervoirs	status	category	(g)	(cm)	weight (g)	an egg (cm ³)	cundity	cundity (g ⁻¹)
Anuradhapura								
Nachchaduwa	M	MAP	165.71 ±	24.57 ±	19.14 ±	$0.07 \pm 0.03^{a,A}$		72.83 ±
			85.06 ^{a,A}	3.96 ^{a,A}	8.86 ^{a,A}		2772.08 ^{a,A}	48.94 ^{a,A}
Mahakanadarawa	M	MAP	240.37 ±	28.53 ±	15.15 ±	$0.09 \pm 0.01^{a,A}$		56.90 ±
			44.69 ^{a,A}	2.31 ^{a,A}	3.33 ^{a,A}		1209.83 ^{a,A}	11.22 ^{a,A}
Mahawilachchiya	M	MAP	$74.20 \pm 3.48^{a,A}$	20.30 ±	7.68 ±	$0.06 \pm 0.01^{a,A}$		102.76 ±
				0.66 ^{a,A}	0.50 ^{a,A}		1153.26 ^{a,A}	18.21 ^{a,A}
Angamuwa	M	MEP	159.09 ±	25.13 ±	15.63 ±	$0.19 \pm 0.13^{a,A}$		45.00 ±
			26.66 ^{a,A}	0.42 ^{a,A}	3.43 ^{a,A}		1386.04 ^{a,B}	10.44 ^{a,A}
Puttalam								
Thabbowa	M	MEP	130.44 ±	$23.1 \pm 3.21^{a,A}$	16.63 ±	$0.10 \pm 0.01^{a,A}$		198.36 ±
			62.09 ^{a,A}		10.03 ^{a,A}		2127.16 ^{a,B}	75.184 ^{a,A}
Mahauswewa	E	MEP	147.78 ±	28.0±4.84 ^{a,A}	17.76±7.4	$0.10 \pm 0.01^{b,A}$		126.12 ±
			30.85 ^{a,A}		9 ^{a,A}		1447.73 ^{b,B}	18.57 ^{b,A}
Saliyawewa	M	MIP	103.37 ±	$22.8 \pm 0.32^{a,A}$		$0.09 \pm 0.01^{a,A}$		50.98 ±
			3.01 ^{a,A}		1.79 ^{a,A}		2069.44 ^{a,AB}	19.56 ^{a,A}
Pahariya	M	MIP	141.53 ±	$24.2 \pm 1.03^{a,A}$		$0.10 \pm 0.01^{a,A}$		93.82 ±
			25.85 ^{a,A}		4.51 ^{a,A}		6722.46 ^{a,AB}	34.09 ^{a,A}
Kottukachchiya	M	MIP	201.24 ±	$26.4 \pm 1.57^{a,A}$		0.10±0.02 ^{a,A}	9366.67 ±	47.31 ±
			32.87 ^{a,A}		7.08 ^{a,A}		2194.18 ^{a,AB}	12.84 ^{a,A}
Hambantota	•							
Ridiyagama	E	MAP	166.60 ±	$25.9 \pm 3.15^{a,A}$		$0.05 \pm 0.01^{b,A}$	15200.00 ±	105.07 ±
			64.22 ^{a,A}		2.57 ^{a,A}		1285.82 ^{b,A}	55.63 ^{b,A}

TABLE 2 Continued.

Location and res-	Trophic	Reservoir	Body weight	Total length		•	Total fe-	Relative fe-
ervoirs	status	category	(g)	(cm)	weight (g)	an egg (cm ³)	cundity	cundity (g ⁻¹)
Weerawila	E	MEP	116.32 ± 29.38 ^{a,A}	23.1±1.44 ^{a,A}	9.70 ± 3.18 ^{a,A}	0.05 ± 0.01 ^{b,A}	10100.00 ± 1331.67 ^{b,B}	89.14 ± 15.55 ^{b,A}
Muruthawela	E	MEP	152.43 ± 80.12 ^{a,A}	24.2 ± 1.52 ^{a,A}	12.20 ^{a,A}	0.05 ± 0.01 ^{b,A}	5662.58 ^{b,B}	210.15 ± 148.19 ^{b,A}
Yodhawewa	E	MEP	126.59 ± 3.17 ^{a,A}	24.1 ± 0.32 ^{a,A}	6.02 ^{a,A}	0.07 ± 0.02 ^{b,A}	2371.36 ^{b,B}	232.24 ± 22.43 ^{b,A}
Bandagiriya	E	MEP	226.50 ± 52.75 ^{a,A}	29.8 ± 1.64 ^{a,A}	1.82 ^{a,A}	0.07 ± 0.01 ^{b,A}	1656.30 ^{b,B}	79.53 ± 22.51 ^{b,A}
Udukiriwala	E	MEP	142.75 ± 36.58 ^{a,A}	23.3 ± 1.40 ^{a,A}	3.63 ^{a,A}	0.12 ± 0.05 ^{b,A}	3516.15 ^{b,B}	134.09 ± 52.57 ^{b,A}
Pahala andara wewa	E	MIP	138.53 ± 7.94 ^{a,A}	24.4 ± 0.68 ^{a,A}	15.36 ± 0.42 ^{a,A}	0.05 ± 0.01 ^{b,A}	9322.22 ± 2338.64 ^{b,AB}	67.55 ± 17.48 ^{b,A}
Monaragala								
Muthukandiya	E	MEP	108.84 ± 16.08 ^{a,A}	$23.1 \pm 0.66^{a,A}$	2.17 ^{a,A}	$0.04 \pm 0.01^{b,A}$	264.58 ^{b,B}	15.73 ^{b,A}
Kiriibban wewa	М	MEP	181.03 ± 20.60 ^{a,A}	26.2 ± 0.31 ^{a,A}	9.76 ^{a,A}	$0.09 \pm 0.03^{a,A}$	3633.38 ^{a,B}	67.83 ± 26.12 ^{a,A}
Urusita	M	MEP	164.49 ± 25.00 ^{a,A}	25.4 ± 1.22 ^{a,A}	13.88 ^{a,A}	$0.10 \pm 0.04^{a,A}$	10136.09 ^{a,B}	121.88 ± 82.81 ^{a,A}
Handapanagala	М	MEP	96.25 ± 34.06 ^{a,A}	21.5 ± 3.47 ^{a,A}	7.13 ^{a,A}	0.05 ± 0.01 ^{a,A}	12644.44 ± 1859.01 ^{a,B}	144.25 ± 62.43 ^{a,A}
Hambegamuwa	М	MEP	194.10 ± 35.03 ^{a,A}	26.9 ± 1.59 ^{a,A}	3.87 ^{a,A}	$0.09 \pm 0.02^{a,A}$	4921.30 ^{a,B}	55.11 ± 17.77 ^{aA,}
Buduruwagala	E	MIP	116.02 ± 20.76 ^{a,A}	23.2 ± 0.95 ^{a,A}	2.64 ^{a,A}	0.04 ± 0.01 ^{b,A}	4306.24 ^{b,AB}	170.36 ± 58.82 ^{b,A}
Habaralu	M	MIP	155.73 ± 40.95 ^{a,A}	25.7 ± 1.23 ^{a,A}	9.82 ^{a,A}	0.15 ± 0.03 ^{a,A}	1,972.68 ^{a,AB}	143.82 ± 52.24 ^{a,A}
Mahawewa	E	MIP	97.63 ± 14.80 ^{a,A}	22.7 ± 2.24 ^{a,A}	$2.70^{a,A}$	$0.06 \pm 0.00^{b,A}$	12922.22 ± 566.99 ^{b,AB}	134.50 ± 22.09 ^{b,A}
Sugaladevi	М	MIP	172.54 ± 72.40 ^{a,A}	23.7 ± 1.73 ^{a,A}	12.58 ± 5.85 ^{a,A}	0.11 ± 0.11 ^{a,A}	9744.44 ± 2898.34 ^{a,AB}	66.54 ± 36.66 ^{a,A}

Values in the same column with different superscripts are significantly different (p < 0.05). Simple letters are used in comparing trophic status, while block letters are used in comparing size categories of the reservoirs.

The total fecundity of GFP concerning length classes ranged between 3633.33 and 15902.38, while the total fecundity with respect to weight classes ranged from 5609.52 to 17003.70. The lowest and highest relative fecundity concerning length classes were 71.77 and 583.19, respectively. Concerning weight classes, they ranged from 140.35 (the lowest) to 616.81 (the highest). Additionally, the total fecundity and relative fecundity of GFP increased with advancements in length and weight classes up to a specific size and subsequently decreased with further increases in length and weight. The highest fecundity and relative fecundity were found in the 24 - 25 cm and 22 - 23 cm length classes, while the highest fecundity and relative fecundity per weight were observed in the 185 - 210 g and 160 - 185 g weight classes, respectively. The highest number of ovigerous GFP was recorded in the 24 - 25 cm length and 110 - 135 g weight classes (Figure 1).

Total fecundity, relative fecundity, and egg volume of the GFP in mesotrophic and eutrophic reservoirs were significantly different (p < 0.05). The total fecundity of GFP differed significantly among the different size categories of the reservoirs (major, medium, and minor) (p < 0.05). The highest total fecundity (16751.52 \pm 6391.33) and relative fecundity (131.49 ± 69.09) were observed in eutrophic reservoirs. Concerning the size categories, GFP inhabiting medium perennial reservoirs showed the highest fecundity (16333.33 ± 7154.71) and relative fecundity (123.18 ± 75.70), while GFP from major perennial reservoirs showed the lowest total fecundity (11519.44 ± 3427.38) and relative fecundity (84.39 \pm 39.15). The total fecundity and relative fecundity of GFP concerning trophic status and reservoir size categories are summarized in Table 3. GFP inhabiting reservoirs with an area of 600 - 800 ha showed the highest total fecundity (19622) (Figure 2).

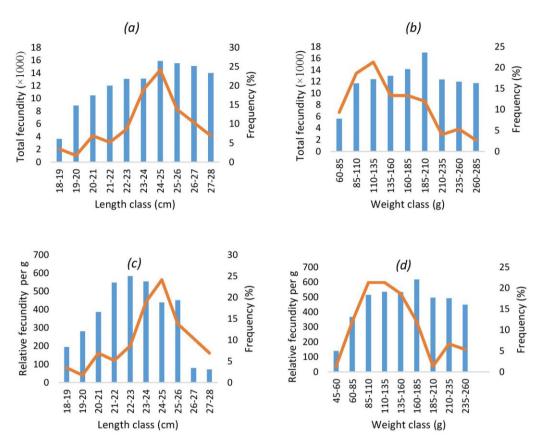


FIGURE 1 Total fecundity and relative fecundity of freshwater giant prawn concerning the length and weight classes. (a) Total fecundity in relation to length classes, (b) weight classes, relative fecundity concerning length classes, and (d) weight classes (columns and solid lines denote total / relative fecundity and frequency, respectively).

TABLE 3 Total fecundity and relative fecundity of giant freshwater prawn collected from different categories of perennial reservoirs in Sri Lanka.

Reservoir category		Total fecundity	Relative fecundity
Trophic status	Mesotrophic	12477.78 ± 6104.90 ^a	90.53 ± 57.52 ^a
	Eutrophic	16751.52 ± 6391.33 ^b	131.49 ± 69.09 ^b
Size category	Major perennial	11519.44 ± 3427.38 ^a	84.39 ± 39.15 ^a
	Medium perennial	16333.33 ± 7154.71 ^b	123.18 ± 75.70°
	Minor perennial	$12568.05 \pm 5795.73^{ab}$	96.86 ± 53.64 ^a

Values for reservoir categories with respect to trophic status or size category in the same column with different superscripts are significantly different (p < 0.05).

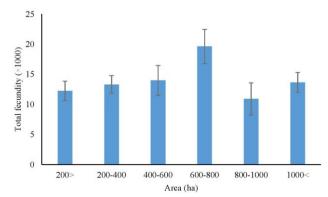


FIGURE 2 Total fecundity of giant freshwater prawn collected from different sizes of reservoirs.

The fecundity of GFP inhabiting mesotrophic and eutrophic reservoirs showed a positive correlation with total length, body weight, and egg mass weight (except for the average volume of an egg). Fecundity in relation to total length and weight, as well as egg mass weight in relation to total length, were more closely correlated in mesotrophic reservoirs than in eutrophic reservoirs. Total fecundity concerning egg mass weight, as well as egg mass weight concerning body weight, was more closely correlated in eutrophic reservoirs than in mesotrophic reservoirs (Table 4). The fecundity of GFP in minor perennial reservoirs showed a strong positive correlation with total length, body weight, and egg mass weight (except for the average volume of an egg), while egg mass weight and

the biometric parameters of GFP in minor perennial reservoirs demonstrated a significant positive correlation (p < 0.05). All correlations for GFP, except egg mass weight vs. body weight in medium perennial reservoirs, were

comparatively lower than in major and minor perennial reservoirs. The correlation of fecundity with other biometric parameters is summarized in Table 5.

TABLE 4 The correlation of fecundity with total length (TL), weight (in g), egg mass weight (EMW, in g) and volume of egg (EV, in cm³) of giant freshwater prawn collected from mesotrophic and eutrophic reservoirs in Sri Lanka.

	Trophic status										
Relations	Mesotro		Eutrophic								
	а	b	R ²	r	р	Α	b	R ²	r	р	
Fecundity vs. TL	-18584	1277.3	0.4847	0.749	<0.001	-18915	1297.8	0.4695	0.685	<0.001	
Fecundity vs. weight	2100	69.058	0.5027	0.709	< 0.001	76.996	92.833	0.4708	0.686	< 0.001	
Fecundity vs. EMW	4429.5	522.38	0.5227	0.663	< 0.001	2,251.3	837.45	0.5871	0.766	< 0.001	
Fecundity vs. EV	12152	6,484.6	0.0033	0.06	0.726	10,040	52,842	0.0531	0.261	0.142	
EMW vs. TL	- 31.68	1.9443	0.754	0739	< 0.001	- 19.654	1.3456	0.6213	0.610	< 0.001	
EMW vs. weight	2.12	0.0885	0.5252	0.632	< 0.001	- 1.2315	0.1058	0.6717	0.638	<0.001	

TABLE 5 The correlation of fecundity with total length (TL, in cm), weight (in g), egg mass weight (EMW, in g), and volume of an egg (EV, in cm³), of giant freshwater prawn inhabiting different size categories of reservoirs.

	Size category											
Relation	Major				Medium				Minor			
	а	b	r	р	а	b	r	p	а	b	r	p
Fecundity vs. TL	-19237	1255.7	0.633	0.001	-15870	1193.5	0.426	0.001	-3254.2	102.22	0.578	0.001
Fecundity vs. weight	3007.3	62.4	0.603	0.001	2685	75.926	0.417	0.001	-30268	1761.2	0.700	0.001
Fecundity vs. EMW	3816.2	653.8	0.509	0.001	5487.1	550.52	0.432	0.001	-21.43	825.54	0.756	0.001
Fecundity vs. EV	6457.7	100320	0.249	0.152	10564	41005	0.117	0.307	-7622.5	39895	0.109	0.491
EMW vs. TL	5.034	0.05	0.501	0.001	5.1842	0.0623	0.287	0.144	-4.6097	0.1275	0.689	0.001
EMW vs. weight	-8.993	0.91	0.411	0.001	-20.758	1.4249	0.420	0.001	-35.623	2.0807	0.724	0.001

4 | DISCUSSION

The present findings elucidate that the total fecundity and relative fecundity of ovigerous GFP significantly differ spatially (among districts) and in relation to trophic status and the area of the reservoirs (size). The highest fecundity in GFP has been observed in the 24 - 25 cm length and 185 - 210 g weight classes, and GFP inhabiting eutrophic medium perennial reservoirs exhibited the highest fecundity. Additionally, fecundity strongly correlates with the length and weight of GFP, as well as the egg mass weight of the individuals. These findings are significant since studies conducted so far have only focused on fecundity and gonad maturation in different species of prawn (Deekae and Abowei 2010; Kumar et al. 2017), while comprehensive studies to ascertain the relationship between the fecundity of GFP and the trophic status and scale of the reservoir are relatively scarce in Sri Lanka. The study confirms that most dry-zone reservoirs are eutrophic, indicating that allochthonous nutrients significantly influence their productivity, which can be assessed through their trophic status. The condition of dry-zone reservoirs enables GFP to grow significantly, resulting in the largest GFP ever recorded globally.

Literature confirms the variation in fecundity among species of *Macrobrachium*. When fully mature, the highest fecundity within the genus has been observed in *M*.

rosenbergii and M. carcinus, which can lay 80000 -100000 eggs during each spawning (Da Silva et al. 2004). Two other studies (Ang and Law 1991) have reported that the fecundity of GFP in wild populations ranges from 60000 to 130000. However, the higher fecundity recorded in the present study is lower than these estimates. Collected GFP from Sri Lankan reservoirs come from culturebased fisheries, where post-larvae are stocked periodically. Thus, ovigerous females collected from fishers' harvest for this study may include females in their first spawning. As a result, the lowest (3208) and highest (31738) fecundity of GFP encountered in this study deviated from the range reported by Ismael and New (2000), which indicated that GFP could lay only 5000 to 20000 eggs in the first spawning. The highest number of eggs in GFP observed at Yodhawewa Reservoir (29366.67 ± 2371.36) exceeds the (11808 ± 8155) eggs per individual GFP reported by Utami and Supratman (2018). In contrast, the fecundity recorded in the current study is lower than that reported by Adha et al. (2016) and Cavalli et al. (2001), at 30633 ± 12068 and 46512 ± 11220 eggs per individual, respectively.

The variations in fecundity may be attributed to different conditions of females maintained in the laboratory, physiological factors, and seasonal changes (Lobao *et al.* 1986). According to Silva *et al.* (2024), DO and turbidity

significantly affect the fecundity and egg development of M. amazonicum, while temperature modulates the incubation period and endocrine-driven gonadal maturation in decapods (Tropea et al. 2015). Additionally, suboptimal pH levels can lead to metabolic stress and reduce the energy available for reproduction in prawns and crayfish (Chen and Chen 2003). Graziani et al. (1993) documented that the fecundity of Macrobrachium species is closely associated with the age of females and increases as the females mature. Additionally, Bal and Rao (1990) stated that individuals of the same prawn species produce different numbers of eggs depending on their age, length, weight, and environmental conditions. The present study reports the highest and lowest relative fecundity (eggs per gram of body weight) in GFP from Yodha Wewa $(232.24 \pm 22.43 \text{ egg g}^{-1})$ and Angamuwa (45.00 ± 10.44) egg g⁻¹). Furthermore, the relative fecundity of GFP reported in the current study is lower than the value (989.57 egg g⁻¹) reported by Sharma and Subba (2005). However, the relative fecundity of M. lamarrei (18.84 egg g⁻¹) reported by Sharma and Subba (2005) is comparatively lower than the lowest relative fecundity (40.61 ± 22.50 egg g⁻¹) reported in this study. As GFP continues to grow larger in Sri Lankan reservoirs, it can be expected that the relative fecundity will be lower compared to the number of eggs produced.

Silva et al. (2004) reported that the average fecundity of M. amazonicum increased continuously with increasing length classes (0.5 cm), with the highest fecundity observed in the 9.5 - 10.0 cm length class, which was the highest value recorded in that study. However, the average fecundity of M. amazonicum did not progressively increase with increasing weight classes (0.5 g). In contrast, the present study found that average fecundity increased with length and weight classes up to a specific size range (24 - 25 cm; 185 - 210 g, respectively) and then decreased after reaching its peak. Nikolsky (1963) reported that fecundity tends to decrease when animals reach a specific size because the number of oocytes produced declines in ageing fish. The results of this study align with life-history theory (Stearns 1992), which predicts that reproductive investment peaks at intermediate sizes due to trade-offs between survival, growth, and reproduction. At larger sizes, declining fecundity may indicate senescence, with energy being redirected toward maintenance rather than reproduction.

Bertini *et al.* (2014) have not found any differences in the fecundity of *M. acanthurus* at relatively moderate or large spatial scales. In contrast, the present study finds that the fecundity of GFP varies with the scale of the reservoirs (major, medium, minor). The highest fecundity of GFP recorded in this study comes from medium perennial reservoirs with a size range of 600 – 800 ha. Consistent with the present study, findings from research on *Macrobrachium* species and other freshwater and marine crus-

taceans have shown differences in fecundity across small, moderate, and large spatial scales (Mashiko 1983, 1990). A comprehensive study (Jones *et al.* 2021) demonstrates that monetary biomass gain, an indirect measure of the economic gain from CBF, is significantly higher in medium reservoirs than in major and minor reservoirs. Fish production in reservoirs is directly linked to the physical, chemical, and biological parameters of those reservoirs. Medium perennial reservoirs provide favourable conditions for production and thus fecundity of GFP, compared to major and minor reservoirs. Overall, the variation in fecundity of GFP relative to reservoir size confirms that environmental conditions, which are not homogeneous throughout the dry zone in Sri Lanka, influence the fecundity of GFP inhabiting those reservoirs.

Moreover, the nutrient status of reservoirs influences the fecundity of GFP. In addition to the quantity and quality of food sources, population density, carrying capacity, and stress from predators affect the health of spawning females, as well as the quality and quantity of the eggs produced (Lardies and Castilla 2001; Lardies and Wehrtmann 2001; Bas et al. 2007; Hjelset et al. 2012; Griffen 2014; Belgrad and Griffen 2016). The sampled reservoirs are trophically categorized based on chlorophyll-a content, which shows 44% eutrophic, while the majority are mesotrophic. Pantaleao et al. (2018) have observed a positive correlation between fecundity and chlorophyll-a concentration. In the current study, the fecundity of GFP inhabiting eutrophic reservoirs is higher than that of mesotrophic reservoirs.

The efficiency of egg production (the number of eggs produced per female unit body weight) may depend on size and/or age and is generally thought to increase with female size (Malecha 1983). However, some studies have demonstrated that female size does not significantly affect egg production efficiency (Rao 1991; Cavalli et al. 2001). In contrast, several studies on various crustaceans have demonstrated that fecundity is closely linked to female size (Nazari et al. 2003; Adha et al. 2016). In the present study, the fecundity of GFP exhibited a strong positive correlation with the size (length, weight) of females in mesotrophic and eutrophic reservoirs, except for medium perennial reservoirs. Mahapatra et al. (1996) and Adha et al. (2016) found that fecundity was more closely related to weight than to the length of the prawn. In this study, this finding coincided only with the results for medium perennial reservoirs; in all other reservoir types, fecundity was more closely related to length than to the weight of GFP. Environmental, genetic, and nutritional factors may lead to different patterns of body sizefecundity relationships, and the egg production efficiency in GFP across different size classes likely depends on several of these factors (Cavalli et al. 2001). Selecting smaller females for hatchery use may provide an advantage due to their high molting frequency, which promotes a high breeding frequency and potentially more efficient egg production. Although smaller females were more efficient in terms of egg production per body weight, producing eggs over time is crucial in hatchery settings. Hence, hatchery operators generally select larger females as brooders, since fecundity is linearly correlated with female size. Several studies (Malecha 1983; Ang and Law 1991; Rao 1991; Kingdom and Eroudu 2013) have observed a positive correlation between fecundity and the egg mass weight of Macrobrachium vollenhovenii. However, no correlation between egg mass weight and female body mass was found in Macrobrachium hainanense by Mantel and Dudgeon (2005). The present study indicates that fecundity strongly correlates with egg mass weight, while egg mass weight and total weight are strongly related to trophic status and minor perennial reservoirs. This study's cross-sectional design and lack of age data limit insights into temporal and age-related patterns of fecundity. Unaccounted genetic and environmental variability may also have influenced results. Future research should consider long-term, age-structured, and genetically informed approaches to gain a deeper understanding of this phenomenon.

5 | CONCLUSIONS

In conclusion, the current findings confirm that fecundity depends on the length, weight, and egg mass weight of the ovigerous GFP. It reveals that the highest fecundity occurs in eutrophic medium perennial reservoirs, within the 24 - 25 cm and 185 - 210 g size range of GFP. These findings support the postulated hypothesis that the fecundity of gravid GFP varies with the trophic status and size of the reservoir where they have been stocked for CBF development. Based on the findings of this study, it is recommended that broodstock be selected from medium-sized eutrophic reservoirs, where higher fecundity was observed. Furthermore, selecting females within the optimal size range (24 - 25 cm and 185 - 210 g) is recommended to maximise reproductive output. They demonstrate the potential for selecting suitable brood stock from the stocked reservoirs, thereby overcoming the difficulties associated with collecting them from wild riverine habitats. These findings may also apply to GFPdependent CBF globally.

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CONFLICT OF INTEREST

The author declares no conflict of interest.

AUTHORS' CONTRIBUTION

Data collection: RGS, AUK, UADJ, and KHMAD; Data anal-

ysis: RGS and AUK; Manuscript preparation: RGS, AUK, UADJ, PLNL and KHMAD; Funding: UADJ and KHMAD.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on a reasonable request from the corresponding author.

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